

THE EVOLUTION OF LIFE HISTORY TYPES IN THE RHODOPHYTA : AN APPRAISAL *

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SUMMARY. — It has been suggested recently that the *Palmaria palmata*- and the *Rhodophysema elegans*-type life histories were derived by evolution from the *Polysiphonia*-type. A more acceptable explanation, on the available evidence, may be that the former two types developed independently of the latter. There is in the Rhodophyta a well defined evolutionary trend towards zygote amplification, probably to compensate for the total absence of the flagellated reproductive bodies. Two mechanisms for this amplification have developed : 1) the formation of a mitosporangial (carposporangial) generation, the spores of which give rise to an independent meiosporangial generation (triphasic); 2) the formation of a meiosporangial generation directly from the zygote (diphasic). It is suggested that the second mechanism has arisen several times in the red algae; in some instances this has been by derivation from the *Polysiphonia*-type, but in the case of many of the primitive *Palmariales* and *Acrochaetiales* it would appear to have arisen independently.

RÉSUMÉ. — Il a été suggéré récemment que les cycles de développement de types *Palmaria palmata* et *Rhodophysema elegans* ont évolué à partir du type *Polysiphonia*. D'après les documents dont nous disposons il serait peut-être plus acceptable de suggérer que ces deux premiers types se sont développés indépendamment du dernier. Chez les Rhodophyta il y a une tendance bien marquée vers l'accroissement du rôle du zygote, ce qui pourrait compenser l'absence totale de corps reproductifs flagellés. Cette amplification serait possible par l'un ou l'autre des deux mécanismes suivants : 1) la formation d'une génération supplémentaire mitosporangiale (carposporangiale) dont les spores produiraient une génération méiosporangiale indépendante (triphase); 2) la formation directe d'une génération méiosporangiale (diphase). Nous suggérons que le deuxième mécanisme est survenu plusieurs fois chez les algues rouges; dans certains cas à partir du type *Polysiphonia*, mais aussi sans doute indépendamment de celui-ci chez les *Palmariales* et les *Acrochaetiales* primitifs.

KEY WORDS : carposporophyte development; evolution of life history; Rhodophyta; tetrasporophyte modification; zygote amplification.

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INTRODUCTION

MAGNE (1982) has contented that two recently-discovered life history types in the Rhodophyta, the *Palmaria palmata*-type (VAN DER MEER and TODD, 1980; DIXON, 1982) and the *Rhodophysemia elegans*-type (DECEW and WEST, 1973, 1982), are derived from the *Polysiphonia*-type (DIXON, 1982). He bases his conclusions largely on the supposed ability of life history phases of red algae to become reduced and, ultimately, parasitic on the preceding generation. More recently, GABRIELSON and GARBARY (1986) have supported this interpretation by saying that «... all sexual life histories in red algae are triphasic or easily derived from triphasic patterns through reduction».

DISCUSSION

— Zygote amplification in the Rhodophyta

Red algae are unique amongst eukaryotic algae in completely lacking flagellated reproductive structures. It has been postulated that the carposporophyte probably evolved *in situ* as a means of zygote amplification (SEARLES, 1980). It seems most unlikely that the red algal carposporophyte was ever represented by a separate, free-living, spore forming phase as advocated by J. FELDMANN (1952), and later by MAGNE (1967, 1972, 1982), ABDEL-RAHMAN and MAGNE (1983) and others.

Hypothetically, two methods of zygote amplification are possible : 1) the production of a meiosporangial generation directly from the zygote, the spores of which give rise to the gametangial phase; 2) the production of a mitosporangial phase from the zygote, the spores forming an independent meiosporangial phase; SEARLES (1980) argues that the latter strategy would, in evolutionary terms, be more successful than the former.

The questions I will discuss here are : 1) did the carposporophyte evolve from a free-living, independent generation, as proposed by FELDMANN (1952) and supported by MAGNE (1972), UMEZAKI (1977) and GARBARY (1978), amongst others; 2) are the tetrasporangia-bearing phases formed directly on gametangial plants all derived from carposporangial phases ?

— Development of the carposporophyte

In order to attempt an answer to the question, did the carposporophyte evolve from a free-living phase, it is necessary to examine some carposporophyte types described for the Rhodophyta and the nature of the carposporangial phase. It should be stressed at this point that DREW (1955) and DIXON (1973, 1982) define a phase as starting with a single reproductive cell or spore and ending with a spore.

ABDEL-RAHMAN and MAGNE (1983) reported that the zygote («sporozygote») in a cultured strain of *Acrochaetium pectinatum* (referred to *Audou-*

nella simplex in GABRIELSON and GARBARY, 1986) is sometimes released without further development; on other occasions the zygote develops *in situ* to form gonimoblast tissue and, ultimately, carposporangia. Separate tetrasporangial plants develop from both the sporozygotes and the carpospores. These authors use this fascinating study to postulate the independent development of red algal carposporophytes instead of concluding that zygote amplification is not universal amongst the Florideophyceae. According to Abdel-Rahman and Magne the «sporozygote» represents a single carpospore formed directly from the fertilized carpogonium and must therefore be considered as the equivalent of a generation. In my opinion this single «carpospore» cannot be regarded as a free-living generation: it is the result of fertilization and develops independently from the gametophyte but gives rise to nothing more than filaments that bear tetrasporangia. It seems appropriate to me that this type of development should occur in a species referred to the Acrochaetiales, as this family is generally agreed to encompass the most primitive extant Florideophyceae, and the ancestral red algae were probably of this type (see GABRIELSON and GABARY, 1986).

Rhodochaete parvula (Rhodochaetales) is sometimes considered to be intermediate between the Bangiophyceae and the Florideophyceae (KRAFT, 1981), although it is always referred to the Bangiophyceae. It possesses apical growth (MAGNE, 1960) and pit connections (BOILLOT, 1978). A trichogyne or pro-trichogyne is not formed and, after fertilization (MAGNE, 1960), the zygote divides into two cells, one of which is released (MAGNE, 1960; BOILLOT, 1975) and thus represents a single carpospore. These carpospores give rise to diploid plants (BOILLOT, 1975) with thicker walls, and lacking any sexual reproductive structures. These plants form monosporangia only, some of which duplicate the diploid sporophyte and some form the gametophyte generation, although the exact site of putative meiosis is unknown. No tetrasporangia are formed, which firmly places the genus in the Bangiophyceae. The life history of *Rhodochaete parvula* is thus triphasic.

The site of meiosis in the Bangiaceae is variable. MIGITA (1967) and GIRAUD and MAGNE (1968) reported stages of reduction division in the conchosporangia of *Porphyra umbilicalis* var. *laciniata* and *P. yezoensis* respectively. MA and MIURA (1984) however provided strong evidence that meiosis in a strain of *P. yezoensis* occurred in the conchospores, and it may be that the site of reduction division in *Porphyra* species is variable depending on strain differences or environmental factors. It is interesting to note, from the point of view of evolution, that monosporangia, both mitotic and meiotic, may occur in species belonging to the Bangiaceae, Acrochaetales and in some families of the Nematiales (Galaxauraceae, Liagoraceae, Nematiales). True monosporangia are absent from the Rhodymeniales and Ceramiales and are quite rare in the Gigartinales *sensu lato* (including the Cryptonemiales; see KRAFT and ROBINS, 1985).

MAGNE (1967, 1972) earlier suggested that *Ahnfeltia plicata* might have a very simple type of life history in which «monospores» give rise directly to

«monospore»-forming plants. This type of life history might, he argued, have been derived from a hypothetical free-living carposporophyte (see MAGNE, 1972, Fig. 18 Nos 9 and 10). Later, FARNHAM and FLETCHER (1976) and CHEN (1977) showed that a crustose, free-living, tetrasporangia-bearing phase occurs in the life history of *Ahnfeltia plicata* and there can be little doubt, therefore, that the «monosporangial pustules» of this species represent cystocarps, albeit of a structure not typical of the Phylloporaceae. These pustules require further investigation.

— Tetrasporophyte modification

In any discussion of the evolution of algal life histories consideration must be given to the nature of the diploid, meiosporangial phase. MAGNE (1972) regards algae with heteromorphic gametangial/meiosporangial phases [(the *Bonnemaisonia hamifera*-type of DIXON (1982) and the *Nemalion*-type of GABRIELSON and GARBARÝ (1986)] as having been derived from algae with *Polysiphonia*-type life histories. It is significant to note that the Rhodymeniales and Ceramiales, widely regarded as the most advanced red algae (e. g. KRAFT, 1982), are known to have only *Polysiphonia*-type life histories; even *Minium*, a recently discovered genus of Rhodymeniales with a crustose growth form, the first such representative of either order, has a *Polysiphonia*-type life history (MOE, 1979). In contrast, the Acrochaetiales and Nemaliales, universally agreed to be the most primitive orders of the Florideophyceae, have numerous representatives with *Bonnemaisonia hamifera*-type life histories and there is more variation in life history pattern in these orders than in any other order of Florideophyceae (UMEZAKI, 1977).

A more satisfactory explanation of the evolutionary development of red algal life histories is that both the *Bonnemaisonia hamifera*-type and the *Polysiphonia*-type life histories arose independently from acrochaetioid ancestors with a low level of vegetative organisation similar to those currently referred to the Acrochaetiales. Considerations such as spore dissemination, increasing surface area/volume ratios, grazing pressure, and the necessary to capture male gametes, dictated the development of various life history types. This particular interpretation would not appear to have been considered previously.

— Origin of carpotetrasporophytes

The second question of crucial importance is: are those meiosporangial phases that are dependent on gametangial plants derived from carposporophytes? Red algae forming what were termed «carpotetrasporangia» by FELDMANN (1939), and which are included by DIXON (1982) in the *Liagora tetrasporifera*-type life history are of two types (MAGNE, 1967): 1) Those that form carposporophyte-like structures formed in «cystocarps»; 2) Those that form structures for which SCHOTTER (1968) coined the term «tetrasporoblasts». Algae of the first type form tetrasporangia terminally on carposporophyte-like structures and most of these have closely related species that form single-spored

carposporangia (e. g. *Liagora*). In the second type of spreading, initially vegetative, thallus is formed over the surface of the gametophyte; this produces tetrasporangia and bears little resemblance to a carposporophyte. However, in a recent study of *Gymnogongrus griffithsiae*, the type species of the genus, CORDEIRO-MARINO and POZA (1981) claimed that gonimoblast filaments grew inwards from the supporting cell and carposporangia developed from these filaments and from medullary cells with which they fused. These carposporangia germinated *in situ* to form an outwardly-growing tissue which ultimately produced an external protuberance (tetrasporoblast) bearing tetrasporangia. This study, although it is not clear exactly how the carposporangia are formed, shows how tetrasporoblastic species of Phyllophoraceae appear to have been derived from closely-related algae with a *Polysiphonia*-type life history. I would, therefore, agree with MAGNE (1967, 1972), SEARLES (1980), and others that this particular mode was derived from algae with a *Polysiphonia*-type life history.

— Life histories in the Palmariales

In contrast, species with *Palmaria palmata*- and *Rhodophysemia elegans*-type life histories have no close relatives with *Polysiphonia*-type life histories; I cannot therefore accept the hypotheses of MAGNE (1982) and GABRIELSON and GARBARY (1986) that they evolved from algae with *Polysiphonia*-type life histories. The unfortunate situation that has arisen with regard to the taxonomic placement of the Palmariales should be noted here. Because of historical connections, the Palmariales has usually been placed between the Rhodymeniales and the Ceramiales (e. g. PARKE and DIXON, 1976; KRAFT, 1981; WYNNE and KRAFT, 1981) or the Palmariaceae are placed in the Rhodymeniales (e. g. CHRISTENSEN, 1980). This is simply not justified; Palmariales has not the remotest taxonomic relationship with either of these patently advanced and highly specialised orders. Indeed, many of its characters point to a very primitive placement. This opinion is borne out by recent studies of the pit-plugs (pit connections) of the Florideophyceae (PUESCHEL and COLE, 1982). The pit-plugs of the Palmariales, Nemaliales and the Acrochaetiales are very similar. The Palmariales should be placed with these two orders and this should serve to dispell the notion that these algae are in any way advanced or show advanced features like those of the Rhodymeniales and Ceramiales. Within this new conceptual framework the taxonomic inter-relationships of the orders of the Florideophyceae should become a little clearer.

Species of Acrochaetiaceae show many other features in common with the Palmariaceae. In particular, one must mention the life histories of *Rhodochorton purpureum* and *R. floridulum* (WEST, 1969, 1970; STEGENGA, 1978; OHTA and KUROGI, 1979). In *R. purpureum*, the fertilized carpogonium gives rise to what has been referred to as a «club-shaped gonimoblast» which grows to four cells long. Tetrasporangia-bearing filaments, which are narrower than the gonimoblast filament, arise from the apical cell. Rhizoids develop from other cells of this filament (STEGENGA, 1978 Figs. 10, 12; OHTA and KUROGI, 1979 Fig. 10) and grow downwards. WEST (1969, 1970) avoided the use of the term

carposporophyte for this clavate structure. FELDMANN (1972) considered the immediate clavate post-fertilization structure to be of little significance («cycle digénétique diplohaplophasique»); MAGNE (1972), on the other hand, had no difficulty in conceiving of a carposporophyte («cycle trigénétique haplodiplophasique») and STEGENGA (1978) more or less agreed with him. In my opinion, a carposporophyte generation similar to that found in algae with a *Poly-siphonia*-type life history cannot be inferred unless that phase releases spores or, at least, forms sporangia which germinate *in situ*. Accordingly, *Rhodochorton purpureum* is best regarded as being diphasic, the spore-forming phase being a tetrasporophyte. OHTA and KUROGI (1979) found that the length of the «gonimoblast» varied in the two Japanese isolates of *R. purpureum* they cultured; in one isolate (monoecious) the «gonimoblast» grew to 230 μm long, was occasionally branched, and formed very few rhizoids; the other isolate (dioecious) had a four-celled, unbranched «gonimoblast» and rhizoidal cells produced from the base also formed «secondary gonimoblasts». In *R. floridulum* (STEGENGA, 1978) a microscopic female gametophyte gives rise directly to a macroscopic tetrasporophyte, in this instance without the intervention of what STEGENGA (1978) calls «clavate gonimoblast cells». The life history of *Rhodochorton floridulum* has also been referred to as being triphasic. This life history is also, in my opinion, diphasic and the two *Rhodochorton* species for which life histories have been worked out in culture are very similar, although the size of the gametangial plants is rather variable. At no time does the gonimoblast tissue formed resemble with any degree of certainty the gonimoblast tissue of other red algae.

In the life history of *Palmaria palmata*, the fertilized carpogonium gives rise directly to vegetative, diploid tissue which ultimately forms tetrasporangia (VAN DER MEER and TODD, 1980; VAN DER MEER, 1981) and no gonimoblast tissue is formed. In *Rhodophysema elegans* (DECEW and WEST, 1982) and probably in *R. georgii* (GUIRY, unpublished), the fertilized carpogonium divides unequally, forming a generative stalk cell and a tetrasporocyte* which divides and forms tetrasporangia. LEE and KUROGI (1978) described a very similar life history in the endophytic species *Rhodochorton subimmersum*, in which the fertilized carpogonium divides directly to form a generative stalk cell and a tetrasporocyte.

A further life history type has recently been discovered in *Coriophyllum expansum*, a species which was placed in the Squamariaceae (= Peyssonneliaceae) until PUESCHEL and COLE (1982) found that it has two layered pit plug caps similar to those found in *Palmaria* and *Rhodophysema*. DECEW (1983) has found that *Coriophyllum* has a life history which may be regarded as intermediate between those of *Rhodophysema* and *Palmaria*. The fertilized carpogonium

* The terminology adopted here is that of PUESCHEL (1979, 1982). A tetrasporocyte is a cell destined to cleave directly to form tetraspores. The terms «mother cell» and «initial» are unsatisfactory as they imply cell division rather than cleavage. A tetrasporangium is a sporangium that cleaves to form four spores.

gives rise to intrusive filaments which, ultimately, spread over the surface of the crustose thallus in a manner similar to the tetrasporoblasts of the Phyllophoraceae. This structure then forms regenerative stalk cells and tetrasporocytes similar to those found in *Palmaria* and *Rhodophysema*. In all these instances a carposporophyte is absent and no gonimoblast tissue is formed. Functionally, *Rhodochorton*, *Palmaria*, *Rhodophysema* and *Coriophyllum* all have a *Palmaria*-type life history if the different sizes of the various phases are discounted. However, the definition of the *Palmaria*-type life history would then be very similar to that described for the *Liagora tetrasporifera*-type by DIXON (1982).

Is it absolutely necessary to separate these two life history types? If it is, it may then be expedient to include two further life history types for *Rhodophysema elegans* and *Coriophyllum expansum* in addition to the five types given in DIXON (1982), and the life history of *Acrochaetium pectinatum* may then be considered to be of the *Polysiphonia*-type (cf. ABDEL-RAHMAN and MARGNE, 1983 and GABRIELSON and GARBARY, 1986). The crucial difference between these life history types is the position of meiosis: in the *Polysiphonia*-type it takes place in fronds similar in morphology to the gametangial plants; in the *Bonnemaisonia hamifera*-type it takes place in fronds dissimilar in morphology to the gametangial plants; in the *Lemanea*-type meiosis takes place somatically during the development of erect fronds; in the *Palmaria*-type it takes place in erect fronds dissimilar in morphology to the female gametangial plants but similar to the male plant; in *Rhodophysema* it takes place in tetrasporangia formed within the carpogonium; in *Coriophyllum* it takes place in a tetrasporangial phase developing over the surface of the gametangial phase. It is possible, however, that *Coriophyllum* could be regarded as having a *Liagora tetrasporifera*-type life history, and *Rhodophysema* as an entirely new type (i. e. meiosis takes place in tetrasporangia formed within the fertilized carpogonium). If the life history of *Coriophyllum expansum* is referred to the *Liagora tetrasporifera*-type life history, it should be with the clear understanding that the similarities are functional rather than taxonomic.

DECEW (1983) discusses the taxonomic placement of *Coriophyllum* and suggests that the genus is best classified as *incertae sedis*. He bases this conclusion on the fact that *Rhodophysema elegans* has been shown to possess B-phycoerythrin whereas *Coriophyllum expansum* has been shown to possess R-phycoerythrin. In a survey of about 50 genera of Florideophyceae, GLAZER, WEST and CHAN (1982) found that both R- and B-phycoerythrins occurred in the species of Acrochaetales* that they examined and concluded: «Phycoerythrins do not appear to be useful at familial, ordinal and class levels in taxonomic studies» (my emphasis). On the basis, however, of the occurrence of B-phycoerythrin, a sexual life history (DECEW and WEST, 1982) and two-layered pit plugs (PUES-

* B-phycoerythrins are considered characteristic of the Bangiophycidae and R-phycoerythrins characteristic of the Florideophycidae. It is not altogether unexpected that a mixture of types would occur in the Acrochaetales and, for that matter, in the Palmariales.

CHEL and COLE, 1982) in *Rhodophysemia elegans**, these authors transferred the genus *Rhodophysemia* to the Acrochaetiales, apparently arguing that as the Palmariales they examined only had R-phycoerythrin, *Rhodophysemia* could not belong to this order. *Rhodophysemia georgii*, the type species of the genus *Rhodophysemia*, has a structure and reproduction more consistent with that of members of the Palmariales, particularly as species currently referred to the Acrochaetiales lack secondary pit connections and cell fusions.

- Validity of the Palmariales

MAGNE (1982) questions the validity of the characters used to separate the Palmariales from the remainder of the Floridophyceae saying that most of these (presence of a regenerative stalk cell; lack of a carposporophyte; lack of a carpogonial branch) are probably the result of evolutionary regression. The principal character used by GUIRY and IRVINE (in GUIRY, 1978) in defining the Palmariales is that of the presence of a specialised regenerative (generative) stalk cell; this is formed by an unequal division of a cortical cell, the outermost cell becoming the tetrasporocyte. On release of the primary tetraspores, the stalk cell divides again, unequally, to form a further stalk cell and another tetrasporocyte (GUIRY, 1974; PUESCHEL, 1979). MAGNE (1982) argues that this is likely to be a derived condition, citing the example of the range of tetrasporangial types found in *Galaxaura* species by SVEDELIUS (1942). Sporangial regeneration is, in fact, a very common feature of the Acrochaetiaceae, Nemaliaceae and Liagoraceae (GUIRY and IRVINE, in press). It seems least specialised in the Acrochaetiaceae where the generative cell is generally identical in morphology to the vegetative cells. In the Galaxauraceae and Palmariaceae, the generative cells are noticeably more specialised, being smaller in size than the vegetative cells. The various types of sporangial regeneration described by SVEDELIUS (1942 Fig. 80) in *Galaxaura* seem to be derived from that found in the Acrochaetiaceae and show increasing elaboration of the generative cells. The illustration of the Acrosporangiate-type by SVEDELIUS (1942 fig. 80, c, d) is misleading in that a series of stalk cells is not built up; instead, a single generative cell elongates with each successive division and ultimately bears a series of soral walls (cf. SVEDELIUS, 1942 Fig. 30). In species of *Palmaria*, *Dewuleraea*, *Halosaccion*, *Leptosarca*, and *Neohalosacciocolax* (Palmariales, Palmariaceae) the tetrasporocyte and the generative cell are enclosed within a common wall (WESTBROOK, 1928; GUIRY, 1976; PUESCHEL, 1979; LEE, 1978; LEE and KUROGI, 1978; GUIRY, 1982). There can be little doubt that this condition is derived from the type of sporangial regeneration found in the Acrochaetiaceae, but I would argue that this is a case of evolutionary progression rather than regression in that the generative cells seem to have become increasingly specialised. Also, it is interesting to note that a series of soral walls similar to those

* *Rhodophysemia elegans* is not the type species of the genus *Rhodophysemia*. The phycoerythrin type of *R. georgii*, the holotype species, is unknown.

of *Galaxaura* species was found in older tetrasporangial plants of *Peyssonnelia immersa* (Peyssonneliaceae) by MAGGS and IRVINE (1983 Figs. 4, 6-8).

The second feature ascribed to the Palmariales by VAN DER MEER (1981) is that of lacking carposporophytes : as I have suggested earlier, MAGNE's (1982) conclusion that this character is derived is not justified on the available evidence. Equally, it cannot be accepted that single-celled carpogonial branches are derived, particularly as they are so common in the Acrochaetiaceae. In the Acrochaetiales and Nemaliales, generally agreed to be the most primitive Florideophyceean algae, no connecting filaments are formed, and, in many species, the carposporophyte arises directly from the fertilized carpogonium. In the Corallinales, Gigartinales (including the Cryptonemiales : see KRAFT and ROBINS, 1985), Rhodymeniales and Ceramiales, connecting cells or filaments are always formed, and thus development of the carposporophyte is exclusively external to the carpogonium.

CONCLUSIONS

In conclusion, several observations can be made. In my opinion, there can be little doubt that *Palmaria* and its relatives are primitive in the accepted sense, and the supposed morphological elaboration of the thalli of these organisms is more apparent than real. The Palmariaceae and certain Acrochaetiaceae appear to have chosen an alternative means of zygote amplification: a means which has not led to as much speciation as the red algal carposporophyte but one which has, nonetheless, survived the ravages of selective pressure. The hypothesis that the carposporophytes of red algae evolved from free-living ancestors is not supported by the available evidence: a more acceptable hypothesis is that these structures evolved *in situ* providing a means of increasing the number of progeny resulting from a single fertilization. Considerably more work is necessary to elucidate the life histories of various Palmariacean and Acrochaetiacean algae before a final phylogenetic scheme can be elucidated.

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